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THE MORPHOLOGY, LIFE-HISTORY, AND TAXONOMIC RELATIONS OF *LEPOCREADIUM AREOLATUM* (LINTON, 1900) STUNKARD, 1969 (TREMATODA: DIGENEA) [1]

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It has long been known that the hydrozoan and scyphozoan medusae and ctenophores of the Woods Hole area harbor unencysted metacercariae of digenetic trematodes. In an abstract, Stunkard (1967) reported natural infections in *Bougainvillia carolinensis, Gonionemis vertens,* and *Chrysaora quinquecirrha.* Infections were found also in ctenophores, *Pleurobrachia pileus, Beroe cucumis,* and *Mnemiopsis leidyi.* He (1978b) reported five species of metacercariae in the ctenophores and medusae of the region. Three species have been identified and their life-cycles have been worked out. Descriptions of the successive stages in the intermediate and final hosts are published: that of *Neopechona pyriforme* (Linton, 1900) by Stunkard (1969b); of *Lepocreadium setiferoides* (Miller and Northrup, 1926) Martin, 1938 by Stunkard (1972); and *Lintonium vibex* (Linton, 1900) Stunkard and Nigrelli, 1930 by Stunkard (1978a). The asexual generations and life-cycle of a fourth species are described in the present report.

Materials and Methods

The metacercariae were found first on 3 August 1973 in specimens of *Mnemiopsis leidyi,* taken in Buzzards Bay, off North Falmouth, Massachusetts. But the identity of the species was quite unknown. Moreover, at least five species of metacercariae were common in the ctenophores and medusae of the area and at that time the life cycles of only two, *Neopechona pyriforme* and *Lepocreadium setiferoides,* had been elucidated. The discovery in 1978 of an ophthalmotrichocercous cercaria in *Nassarius trivittatus,* whose structure agreed with that of the metacercaria, first collected in 1873, led to the resolution of the life-history. Incidence of infection by this species is very slight; the cercaria had not been found in the examination of thousands of specimens of *N. trivittatus.* Only one infected snail was found in 1978 and only one in the examination of hundreds of snails in 1979. The adults produce very few, very large eggs, (Figures 8–11). It should be noted that *N. trivittatus* harbors the asexual stages of another digenetic trematode; an unidentified hemiurid species.

The cercariae are produced in rediae in the haemocoele of the snail. Haemal sinuses contain rediae of various sizes and maturing cercariae (Figure 1). The presence of daughter rediae demonstrates more than one generation of rediae. The cercariae leave the redia in very immature condition, when the eye-spots are circular, pin-head units, and the tail is a non-motile appendage. They mature in the haemocoele and shortly before emergence, setae appear on the tail. They leave the snail through the gills, during the night or early morning and swim at all

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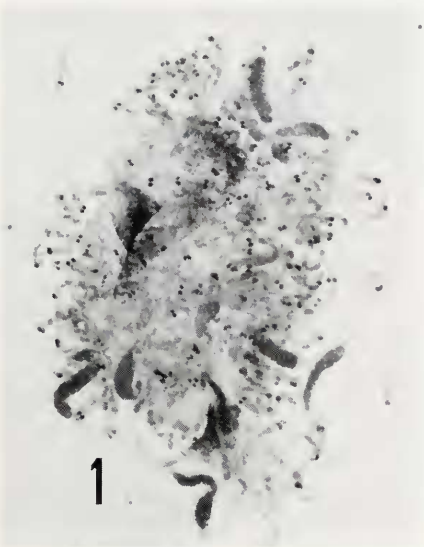

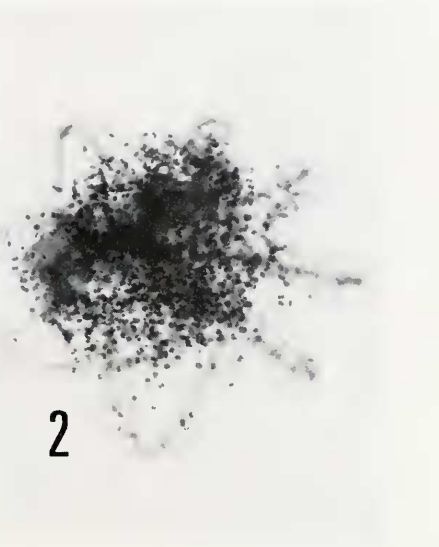

FIGURE 1. Microphotograph, haemal sinus from a specimen of *N. trivittatus*, with immature rediae and cercariae.

FIGURE 2. Microphotograph, intense infection of *Pleurobrachia pileus* exposed two hours to cercariae from *N. trivattatus*.

levels in the water. In swimming, the body is contracted, bent ventrally, the tail is extended and lashes so fast that only a blur appears. They tend toward the light side of the container. They swim with the tail in advance and when contact with a medusa or ctenophore is made, the tail adheres and the cercaria turns to bring the anterior end of the body in position for attachment. By movements of the tail and body, the body penetrates the jelly and the contents of the penetration glands are extruded. When the body is firmly embedded, the activity of the tail frees it from the body and it swims away. When a specimen of *Beroe cucumis* was placed in a bowl with swimming cercariae, they entered the grooves beside the comb-rows, penetrated, and migrated in the jelly. They did not penetrate the pigmented areas between rows. As the cercariae age, they move lower in the water and eventually sink to the bottom. The snail collected at Quissett on 20 July 1978 was shedding and continued to liberate cercariae every day until it was killed on 2 September to get the rediae and developing cercariae, (Figure 1). The snail taken 7 June 1979 was shedding and it continued until 20 July, after which no more cercariae appeared, although it was kept in cool running water and fed daily. It was crushed and examined on 17 August 1979 and contained about sixty rediae but no cercariae, either in the haemocoele or in the rediae. The liver was moribund, lacking in firm consistency and typical cellular organization, and the rediae contained only germ balls. It is well known that when a host is not properly nourished, trematode reproduction is retarded or ceases, and remains dormant until the host recovers its health and vigor. In this instance, it appears that the tissues of squid, clams, hermit crabs and small fishes, fed to the snail, were lacking in some vitamin or other substance essential for the complete metabolic requirements of the snail.

For experimental infection, it is essential to have hosts that are known to be free of previous exposure, or to produce massive infections that can not be miscon-

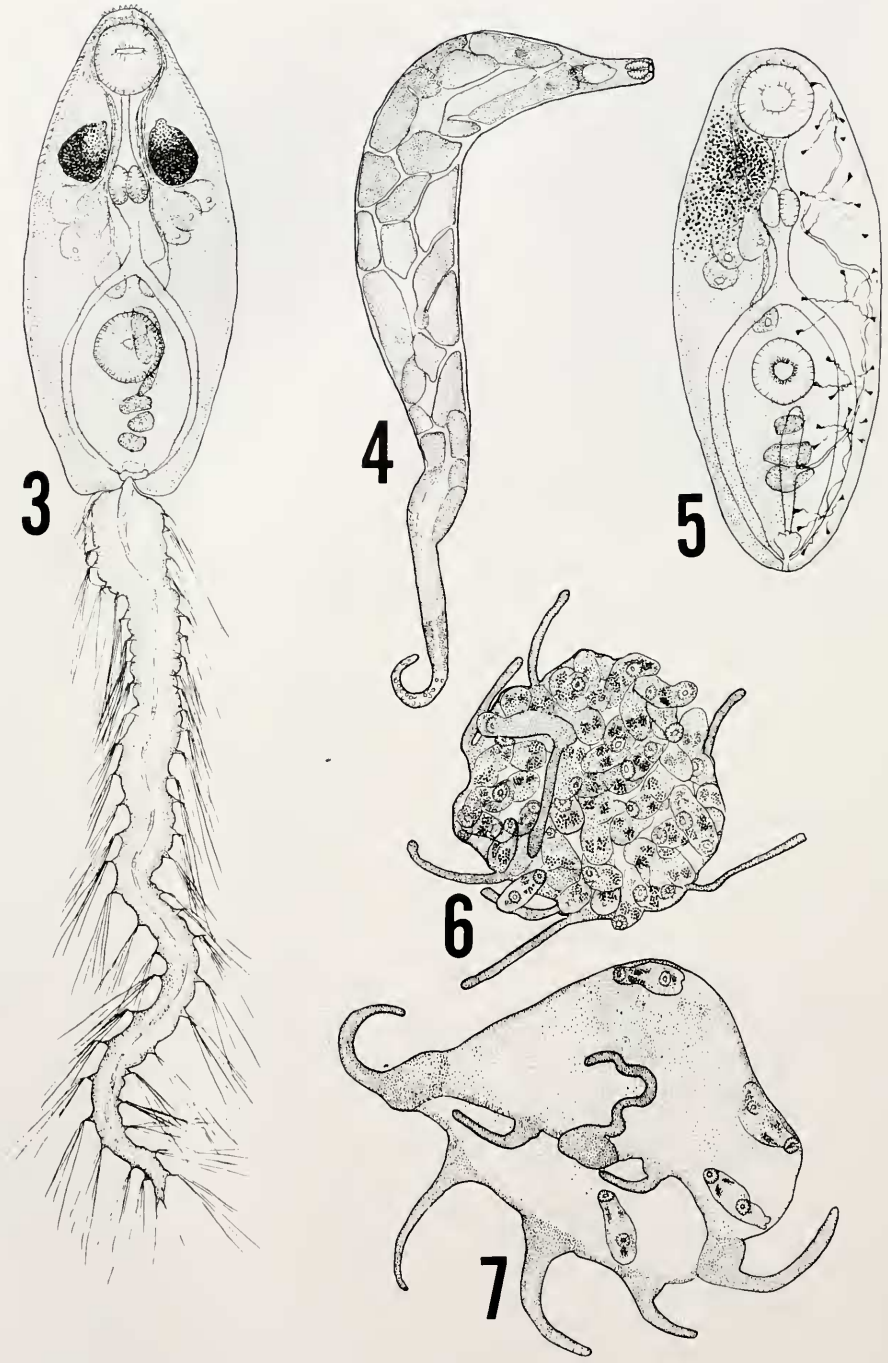

FIGURE 3. Cercaria from *N. trivittatus*, fixed, stained and mounted.
FIGURE 4. Redia from *N. trivittatus*, fixed, stained and mounted.
FIGURE 5. Metacercaria from *Mnemiopsis leidyi*, composite drawing from sketches of living specimens, showing penetration glands and details of the excretory system.

strued (Fig. 2). The ctenophores and medusae from plankton collections contain metacercariae which presage the possibility of error in subsequent interpretation. Crowell (1945) reported that *Podocoryne carnea* lives on the shells of *N. trivittatus,* especially on shells that are occupied by hermit crabs. A unique ecological situation obtains in nature; the snail harbors the trematode which liberates cercariae; the hydroid liberates medusae, which are attacked and penetrated by the cercariae (Figs. 6 and 7). Medusae of *P. carnea,* produced in the laboratory and known to be free of infection, were exposed to cercariae from *N. trivittatus,* and later, embedded in bits of squid or clam, were fed to cunners, *Tautogolabrus adspersus,* that had been maintained for about one month in the laboratory, during which time any natural infections would have matured. Fed twice a week, the method yielded juvenile and gravid specimens of *Lepocreadium areolatum,* a species described initially from white perch and cunners by Linton (1900, 1901), and known also from puffers, *Spheroides maculatus,* and other fishes.

Results and Descripitions

The Adult. (Figures 8–11).

Fixed, stained and mounted specimens may be 1.4 mm long and 0.60 mm wide but most are less than 1.00 mm in length. The largest of the four specimens from the cunner, taken by Linton in 1899 and deposited in the U. S. National Museum under the number 8280, is shown in Figure 10. It is 1.10 mm long and 0.50 mm wide. The worms become mature at a much smaller size and the one from a puffer, shown in Figure 8, with only two eggs, is 0.40 mm long and 0.22 mm wide. The one egg that has a shell, is 0.12 by 0.07 mm; the same size as eggs in larger specimens. In this species the acetabulum is situated about one-third of body length from the anterior end and is somewhat smaller than the oral sucker. Measurements of the holotype were given by Stunkard (1969a). Other specimens are depicted in Figures 9 and 11.

The redia. (Fig. 4).

The rediae are cylindrical, attenuated at both ends, with a curved, pointed, tail-like posterior region. They vary in size from small individuals, 0.20 by 0.04 mm, with germinal cells and a few forming germ-balls to others 1.60 mm long and 0.20 mm wide, filled with germ balls and developing cercariae. The pharynx is spherical to oval, typically longer than broad, 0.048 to 0.058 mm long and 0.030 to 0.040 mm wide. The caecum is small, slightly larger than the pharynx, but displaced and inconspicuous when developing cercariae impinge on the pharynx.

The cercaria. (Fig. 3).

The cercariae are distomate, ocellate, and trichocercous. The body is oval to ovate, somewhat pointed anteriorly. Fixed and stained specimens average 0.38 mm long and 0.16 mm wide. In living specimens the body may be longer and narrower or shorter and wider. The acetabulum is about 0.05 mm in diameter,

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Figure 6. Medusa of *Podocoryne carnea,* intense infection after exposure two hours to cercariae from *N. trivittatus.*

Figure 7. Medusa of *Podocoryne carnea,* slight infection, with four metacercariae of *Lepocreadium areolatum.*

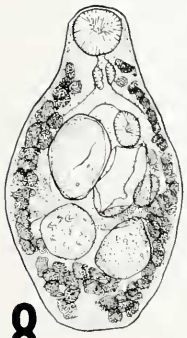
situated in the posterior half of the body; the distance from the anterior end to the acetabulum is about twice as long as the distance from the acetabulum to the posterior end. The opening of the sucker is equipped with a double row of small alternate spines. The tail is 0.45 to 0.54 mm long, 0.05 mm wide at the base, and tapers distally. There is a row of nuclei along the median line and several near the tip. There are twenty-seven pairs of setae and a terminal tuft. The lateral setae have a dorso-ventral alignment and arise from bulb-like expansions of the wall of the tail. They are 0.08 to 0.10 mm long; the terminal ones somewhat shorter. In the anterior fourth of the body the tegument is spined. The ocelli are 0.05 mm long and 0.035 mm wide, situated obliquely, so that the anterior tips are directed mediad. They are separated by about the width of an ocellus. There are four pairs of penetration glands, whose ducts stain with neutral red. One pair is median, below and slightly posterior to the intestinal caeca. Their ducts pass forward under the caeca. There are three pairs anterior and lateral in position; the ducts from the penetration glands pass on the median sides of the ocelli and open near the anterior tip of the body. The oral sucker is subterminal longer than wide and 0.05 to 0.06 mm in diameter. The prepharynx is about as long as the diameter of the oral sucker. The pharynx, situated between and behind the ocelli, is 0.035 mm in diameter. The esophagus, lined with epithelium, is about as long as the prepharynx and the bifurcation of the digestive tract is near midbody, anterior to the acetabulum. The caeca are long and communicate by short, narrow ducts with the posterior end of the excretory vesicle. The intestinal contents stain with neutral red, and when a stained, living specimen is pressed under a coverglass, pink material from the caeca is extruded through the excretory pore. Details of the excretory system were observed in the cercariae and metacercariae. The flame-cells and capillaries in the region of the oral sucker and pharynx were studied in the cercaria, while the ocelli are intact; dispersal of pigment in the metacercaria obscures the excretory structures in this area. The excretory pore is closed by a strong sphincter and the vesicle extends forward to the level of the acetabulum. Collecting ducts open into the vesicle about midway between the acetabulum and the sphincter. The ducts pass forward, turn laterad at the level of the acetabulum under the caeca and continue to the level of the ocelli. Here they turn posteriad and receive a branch from the region of the oral sucker, another from the postoccular area, and a third from the preacetabular region. There each receives the duct which drains the postacetabular area. There are six sets of five cells, as shown in the figure of the metacercaria and the flame-cell formula is $2[(5+5+5)+(5+5+5)]$.

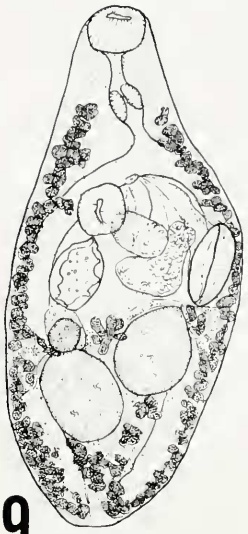
The metacercaria. (Figure 5).

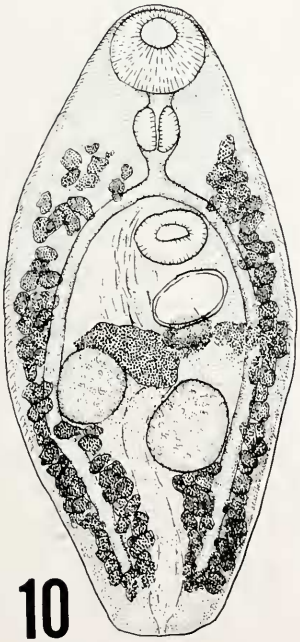
In the ctenophores and medusae, which according to Joyeux and Baer (1961, p. 451) serve as "hôtes d'attente ou paraténique," the cercariae mature but do not increase much in size. The ocelli disintegrate and the pigment is dispersed. Growth occurs primarily in the posterior half of the body; the gonads which are very small in the cercaria, double in size. In the posterior half of the body the flame-cells and capillaries are resolved more readily in the metacercaria than in the cercaria, but the pattern does not change.

Systematic Relations and Discussion

Linton (1900) identified specimens from the white perch, *Morone americana*, taken 27 August 1898 at Woods Hole, as *Distomum areolatum* Rudolphi, 1809.







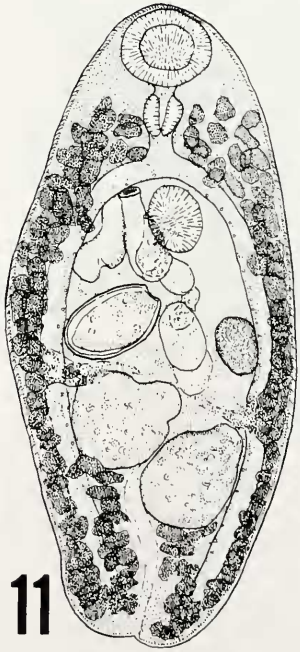


FIGURE 8. *Lepocreadium areolatum*, specimen from *Spheroides maculatus*, 0.40 mm long.
FIGURE 9. *L. areolatum*, specimen from *Spheroides maculatus*, 0.92 mm long.
FIGURE 10. *L. areolatum*, from *Tautogolabrus adspersus*, specimen number 8280 in the U. S. National Museum, 1.10 mm long.
FIGURE 11. *L. areolatum*, from *T. adspersus*, experimental infection, 0.74 mm long.

The worms were found in a dish in which the viscera of the fish had been lying, and the determination was admittedly doubtful. The description was supplemented by Figure 60, Plate 39, and a representative specimen, stained and mounted, was deposited in the U. S. National Museum under the number 6517. The description was based on the mounted specimen, whose measurements were given. Linton (1901), without description or figure, identified, p. 462, specimens taken 5 August 1899 from the cunner, *Tautogolabrus adspersus,* and p. 486, specimens taken the same date from the winter flounder, *Pseudopleuronectes americanus,* as *Distomum areolatum* Rudolphi. The specimens from the cunner were deposited in the U. S. National Museum under the number 8280.

In a report on parasites of fishes taken in July and August, 1901 and 1902, at Beaufort, North Carolina, Linton (1905) identified as *Distomum areolatum* Rud., specimens from *Bairdiella chrysura, Micropogon undulatus, Orthopristis chrysopterus,* and *Sciaenops ocellatus.* The descriptions are too sketchy to have taxonomic value, but the report of infection in *B. chrysura* was supplemented by three figures.

In a posthumous publication, Linton (1940) reviewed, redescribed and reallocated the trematodes from fishes, mainly from the Woods Hole region, that he had assembled in the previous more than 40 years. In the genus *Lepocreadium* Stossich, 1904, he recognized three species: (1) *Lepocreadium pyriforme* (Linton, 1900) described originally as *Distomum pyriforme* n. sp., from the rudderfish, *Palinurichthys perciformis;* (2) *Lepocreadium retrusum* n. sp., from the chub mackerel, *Pneumatophorus grex;* and (3) *Lepocreadium trullaforme* n. sp., from the long-spined sculpin, *Acanthocottus octodecimspinosus,* and other fishes.

Linton's description of *Lepocreadium trullaforme* n. sp., comprised worms collected at different times and from various species of fishes. It included specimens from the long-spined sculpin, *A. octodecimspinosus;* four worms taken 26 April 1915, including the holotype, were deposited in the U. S. National Museum under the number, 8276. Although a specimen from *A. octodecimspinosus* was designated as holotype of *L. trullaforme,* that specimen was not figured; instead, Figure 54 of a worm from *Morone americana* and Figures 53, 55, and 56 of specimens from *Menticirrhus saxatilis* were used to illustrate the morphology of *L. trullaforme.*

In the new species, Linton included: (1) the specimens from *Morone americana,* described (Linton, 1900, p. 293, Figure 60, Plate 39, U. S. National Museum, number 6517, as *Distomum areolatum* Rudolphi; (2) two specimens from the American sole, *Achirus fasciatus,* reported as *Distomum* sp. in Linton (1901, p. 487, Figure 351, Plate XXXI) with types in the U. S. National Museum, number, 8275; (3) one specimen from the kingfish, *Menticirrhus saxatailis,* taken 11 September 1907, in U. S. Museum, number 8277; (4) many specimens, some immature, from young kingfish, *M. saxatilis,* collected 21 August 1918, in U. S. National Museum, number 8278; (5) eight specimens from the white perch, *M. americana,* collected 8 August 1910, in U. S. National Museum, number 8279; (6) specimens from the winter flounder, *Pseudopleuronectes americanus,* collected 5 August 1899, no description or figure, listed as *Distomum areolatum* Rudolphi in Linton (1901, p. 486); and (7) specimens from the cunner, *Tautogolabrus adspersus,* collected 5 August 1899, listed as *Distomum areolatum* Rudolphi (Linton, 1901, p. 462) in U. S. National Museum, number 8280.

Sogandares-Bernal and Hutton (1960) reviewed the genus *Lepocreadium;* they redescribed and figured *Lepocreadium trullaforme* from the holotype, but

the host was given as the cutlassfish, *Trichiurus lepturus*, and the locality as Woods Hole, Massachusetts. They predicated, p. 277, "Linton (1940) pictured different species under the name *L. trullaforme*. We have examined Linton's material and find that he had identified at least two different species as *L. trullaforme*". They recounted the specific features of the species and described the single specimen from the kingfish, deposited in the U. S. National Museum under the number 8277, as a new species, *Lepocreadium caballeroi*.

In an earlier report, Sogandares-Bernal and Hutton (1959) described *Lepocreadium floridanus* n. sp., and devised a key to *Lepocreadium* and closely related genera. In *L. floridanus* the ovary is lobed. They noted, p. 58, "In connection with species of *Lepocreadium* with unlobed ovaries, *L. archosargi* and *L. micropogoni* are probably synonyms of *L. ovale*. A restudy of the type specimens of all three species would be necessary in order to confirm this point." Later, they (1960) examined these holotypes but apparently did not resolve the problem. It should be noted that *L. ovale* Manter, 1931; *L. archosargi* Pearse, 1949; *L. micropogoni* Pearse, 1949; like *L. caballeroi* Sogandares-Bernal and Hutton, 1960, were described from single specimens. The descriptions of *L. archosargi* and *L. micropogoni* as given by Pearse (1949) do not portray specific differences and the holotype of *L. micropogni* was reported by Sogandares-Bernal and Hutton (1960, p. 280) to be in such poor condition that they suggested it be regarded as *species inquirende*. They noted, p. 280, "*L. archosargi* appears to be closely related to *L. caballeroi*, but differs by possessing a cirrus sac which hardly extends posterior to the acetabulum, more anterior vitellaria, and by the presence of ani. Both *L. archosargi* and *L. caballeroi* share the distinction of having eggs which are longer than the acetabulum." *Lepocreadium archosargi* was distinguished from *L. ovale* by what are regarded as trivial and dubious differences. *Lepocreadium ovale* Manter, 1931 was based on a worm from the pinfish, *Lagodon rhomboides* at Beaufort, North Carolina, and as noted by Sogandares-Bernal and Hutton, is probably identical with the worms described by Pearse (1949).

The small worms from a young kingfish, 55 mm long, collected 21 August 1918, number 8278 in the U. S. National Museum, were redescribed by Linton (1940). He noted, p. 90, "A characteristic feature of these distomes is the large size and small number of the ova. No more than two ova were seen in any one of them. Some of the smallest were immature, and contained no ova, but ova were present in quite small specimens. Thus, one, length 0.28 mm., breadth, 0.27 mm., contained one ovum, 0.10 by 0.06 mm., another, length, 0.28 mm., breadth, 0.25 mm., contained two ova 0.10 by 0.05 mm., and 0.10 by 0.06 mm." These worms depicted on Plate 6, Figures 55 and 56, agree so completely with the description and figures of *Lepocreadium setiferoides* (Miller and Northup, 1926) Martin, 1938 as given by Stunkard (1972) that their identity is apparent. The morphology is supported by data from the life-history. Linton (1922) reported on the food of young winter flounders. After listing the secondary intermediate hosts of *L. setiferoides*, Stunkard (1972) observed, p. 329, "The nature of the secondary intermediate hosts probably explains the observations of Linton (1922) and Martin (1938) that infection occurs only in young and small fishes, since older fishes, six to eight inches in length, feed on other and larger organisms."

The specimens from *Morone americana* collected 8 August 1910, in the U. S. National Museum under number 8279, conform to the description of *Distomum areolatum* Rudolphi, collected from the same host-species, 26 August 1898.

The specimens from the winter flounder, *P. americanus*, taken 5 August 1899, without description of figure, were listed as *Distomum areolatum* in Linton (1901, p. 486); their identity is indeterminate.

Specimens from the cunner, *Tautogolabrus adspersus*, in the U. S. National Museum under number 8280, were included in *L. trullaforme* by Linton (1940). They were collected 5 August 1899 and assigned by Linton (1901, p. 462) to *Distomum areolatum* Rudolphi. There are four worms on the slide; the most representative one is shown as Figure 10 in this report.

It may be significant that the several worms, taken at different times from various species of fishes, and identified originally as *Distomum areolatum* Rudolphi, were assigned by Linton (1940) to the new species, *Lepocreadium trullaforme*. Sogandares-Bernal and Hutton (1960) demonstrated that they are not identical with *L. trullaforme*, but the possibility remains that some of them may be included in a common species. The first of these specimens, identified as *Distomum areolatum* Rudolphi, was taken 27 August 1898 from the white perch, *M. americana*. The description was based on a mounted specimen, depicted as Figure 60, Plate 39, and deposited in the U. S. National Museum under the number, 6517. It was restudied by Stunkard (1969a), who recognized it as a member of the genus *Lepocreadium* and designated it as type of *Lepocreadium areolatum* (Linton, 1900) n. comb., adopting the specific name proposed by Linton. It should be noted that the eggs were few and very large, 0.115 by 0.070 mm.

The species includes specimens of natural infection, taken by the writer over the years from cunners, *T. adspersus*, and from puffers *Spheroides maculatus* (Figs. 8 and 9) and after experimental infection of cunners (Fig. 11). The species with large eggs, *L. ovale, L. archosargi, L. micropogoni*, and *L. caballeroi* are very similar and specific identity is not excluded. Linton (1905) reported *Distomum areolatum* from *Orthopristis chrysopterus, Bairdiella chrysura, Micropogon undulatus*, and *Sciaenops ocellarus* at Beaufort, North Carolina. In each instance, the eggs were few and large, 0.120 by 0.070 mm. Linton's (1901, Fig. 346) of *Distomum* sp., which Manter assigned to *L. ovale*, agrees so completely with the description and figures of *L. areolatum* that specific identity is probable. Although the evidence is not final, there is reason to regard *L. ovale, L. archosargi, L. micropogoni*, and *L. caballeroi as* synonyms of *L. areolatum*.

Summary

Digenetic trematodes from the white perch, *Morone americana*, were identified by Linton (1900) as *Distomum areolatum* Rudolphi, 1809. He (1901) referred specimens from the cunner, *Tautogolabrus adspersus*, and the winter flounder, *Pseudopleuronectes americanus*, to the same species. These worms were collected at Woods Hole, Massachusetts. Other specimens were taken from *Bairdiella chrysura, Micropogon undulatus, Orthopristis chrysopterus*, and *Sciaaenops ocellatus* at Beaufort, North Carolina. Linton (1940) included all these worms in a new species, *Lepocreadium trullaforme*. But they are not specifically identical with *L. trullaforme* and their taxonomic status has been uncertain. The metacercariae of these worms have been known for many years an unencysted distomes in the ctenophores and medusae taken in plankton collections. The discovery of an ophthalmotrichocercous cercaria from *Nassarius trivittatus* with the same morphology, has led to the completion of the life-cycle and the resolution of the taxonomic status of the species, which proved to be *Lepocreadium areolatum*

(Linton, 1900) Stunkard, 1969. Cercariae from *N. trivittatus* penetrated and matured in medusae of *Podocoryne carnea,* maintained in the laboratory. Experimentally infected medusae were fed twice a week to cunners, which had been isolated for more than a month, and a series of developmental stages from juveniles to gravid worms were recovered. All stages in the life-cycle are described and figured.

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